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A new genus of Parastenocarididae (Copepoda, Harpacticoida) from the Tocantins River basin (Goiás, Brazil), and a phylogenetic analysis of the Parastenocaridinae

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Abstract

Eirinicaris antonioi **gen.** et **sp. n.** (Parastenocaridinae) is described from the Brazilian rocky savannas, an ecosystem under heavy anthropogenic pressure. The subfamily is distributed worldwide, with representatives in Africa, Asia, Australia, Europe, and North America. This is the first time a non-*Remaneicaris* Parastenocaridinae is described from a Neotropical region indicating that Parastenocaridinae species were already present in a vast geographical area, before the split of the Gondwana. The new taxon is included within the subfamily Parastenocaridinae based on the following characters: 1) segments 5, 6, and 7 of the male antennules forming a functional unit for clasping the female; 2) segment 7 with small process at the inner margin, forming an incipient "pocket-knife" structure with segment 6; 3) last segment pointing medially when closed; 4) the endopod of female leg 3 one-segmented and spiniform, without distal seta; 5) the apophysis and terminal seta of the exopod of male leg 3 are fused; 6) the genital field is rectangular and much broader than the height in the female; 7) the group of three lateral setae I, II, and III of the furca and the dorsal seta are situated at the same level in the female; and 8) the basis of leg 1 has an inner seta. The new taxon can be distinguished from all other Parastenocaridinae genera by the unique sexually dimorphic telson and furca. In the male, the dorsal seta is inserted at the midlength of the furca and setae I, II, and III are displaced anteroventrally. A phylogenetic analysis of the subfamily Parastenocaridinae is given based on the description of the type species of each genus and available descriptions of all Parastenocaridinae species. *Eirinicaris* gen. n. is the sister taxon of a clade formed by *Kinnecaris* and *Monodicaris,* sharing with them the long male and female leg 5 with a long spiniform process, and with *Kinnecaris*, a distal pore on the spiniform process.

Introduction

Copepods of the family Parastenocarididae Chappuis, 1940, are typical representatives of fresh groundwater meiofauna (Corgosinho and Martínez Arbizu 2005). They can be found in different microbiotopes such as the hyporheic zone of alluvial aquifers along rivers, lakes and human-made structures such as dug or artesian wells, as well as associated with mosses and other semi-terrestrial environments such as phytotelmata (Menzel 1916, Chappuis 1931, Jocque et al. 2013).

The taxonomy and phylogenetic relationships among the species of Parastenocarididae are far from resolved with many genera being potentially paraphyletic or polyphyletic. Most of the confusion can be attributed to Jakobi (1972) who divided the family into 26 genera using

a very unorthodox model and was strongly criticized by Schminke 1976. Consequently, the use of Jakobi's (1972) generic names (i.e. *Michelicaris* Jakobi, 1972; *Stammericaris* Jakobi, 1972; *Minutacaris* Jakobi, 1972; *Nanacaris* Jakobi, 1972; *Clujensicaris* Jakobi, 1972; *Phreaticaris* Jakobi, 1972; *Pannonicaris* Jakobi, 1972; *Proserpinicaris* Jakobi, 1972; *Italicocaris* Jakobi, 1972; *Fontinalicaris* Jakobi, 1972; *Entzicaris* Jakobi, 1972; *Lacustricaris* Jakobi, 1972; *Nipponicaris* Jakobi, 1972; *Oshimaensicaris* Jakobi, 1972; *Biwaecaris* Jakobi, 1972; *Enckellicaris* Jakobi, 1972; *Brinckicaris* Jakobi, 1972; *Kinnecaris* Jakobi, 1972; *Cafferocaris* Jakobi, 1972; *Macacocaris* Jakobi, 1972; *Remaneicaris* Jakobi, 1972; *Brasilibathynellocaris* Jakobi, 1972; *Pararemaneicaris* Jakobi, 1972; and *Siolicaris* Jakobi, 1972) was avoided and all species were included in the genus *Parastenocaris* Kessler, 1913, until Corgosinho and Martínez Arbizu (2005) redefined the genus *Remaneicaris,* highlighting the validity of all genera defined by Jakobi (1972). It is important to note the seminal work of Reid (1995), who redescribed *Parastenocaris brevipes* Kessler, 1913, and redefined Lang's (1948) *P. brevipes*-group, calling for a resolution of the taxonomy within the Parastenocarididae. Recently, Schminke (2010) shed more light on this subject and divided the family into two monophyletic subfamilies, Parastenocaridinae Chappuis, 1940, and Fontinilicaridinae Schminke, 2010, both well-defined by strong synapomorphies (Ranga Reddy et al. 2014).

Many genera were revised or proposed recently (viz. Cottarelli et al. 2010, Corgosinho et al. 2008, 2010a, 2012a, b, Karanovic and Cooper 2011, Karanovic et al. 2012, Schminke 2008, 2009, 2013, Ranga Reddy et al. 2014, 2016). Most of these contributions addressed some taxonomic uncertainties in Parastenocarididae by defining real monophyletic groups with clear geographical distributions. With exception of the monospecific genus *Iticocaris* Corgosinho, Martínez Arbizu & Previattelli, 2012, and the genus *Brasilibathynellocaris* from the neotropics, the remaining genera proposed or revalidated recently (i.e. *Stammericaris*, *Kinnecaris*, *Siolicaris*, *Proserpinicaris*, *Remaneicaris, Monodicaris* Schminke, 2009; *Asiacaris* Cottarelli et al., 2010; *Dussartstenocaris* Karanovic & Cooper, 2011; *Horstkurtcaris* Karanovic & Lee, 2012; *Cottarellicaris* Schminke, 2013; *Himalayacaris* Ranga Reddy, Totakura & Corgosinho, 2014; *Indocaris* Ranga Reddy, Totakura & Shaik, 2016), have European, Asian, African and Australian representatives.

The Neotropical fauna of Parastenocarididae is represented by the genera *Remaneicaris*, *Murunducaris* Reid, 1994, *Brasilibathynellocaris*, *Siolicaris*, *Iticocaris*, *Forficatocaris* Jakobi, 1972, and *Potamocaris* Dussart, 1979. With the exception of *Remaneicaris*, all the remaining genera belong to the subfamily Fontinalicaridinae.

In order to improve our knowledge on the biodiversity of Brazil, the National Council of Scientific Research (CNPq) launched in 2010 a call for proposals, to assess the biodiversity of neglected taxonomic groups in understudied Brazilian ecosystems. Our project focused on the microcrustaceans from the Brazilian rocky savannas. These environments fall into the category of azonal biomes (Walter 1985), which during the Pleistocene, extended to the lowlands of what today is occupied by the savanna ecosystems of Cerrado and Caatinga. Nowadays they appear as insular ecosystems at the top of hills, 800 m MSL (above the sea level). This biome is under high anthropogenic threat (Da Silva and Bates 2009) and is the source of headwaters of important Brazilian rivers such as São Francisco, Paraguay, Paraná and Tocantins, connecting biogeographical zones and biomes to the north, south and east of South America.

This contribution describes one of the several new species and genera discovered during an intensive sampling effort conducted in 12 rocky fields in the Brazilian inland. A non-*Remaneicaris* Parastenocaridinae is described from a Neotropical region for the first time and its phylogenetic position within the Parastenocaridinae is discussed.

Material and methods

Specimens of an undescribed taxon were found associated with moss in the littoral zone of the Água Fria River, tributary of the São Bartolomeu River, Tocantins hydrographic basin, 1230 m MSL. The sampling station, characterized by a rocky riverbed, is located at Chapada dos Veadeiros, Alto Paraíso de Goiás, Goiás State, Brazil: 14°5'30.89"S, 47°29'34.47"W (Fig. 1).

Samples of damp moss living next to the waterline were collected on August 12, 2012. The material was concentrated using a 50 µm mesh size net and preserved in 4% formalin. Animals were stained with rose Bengal and sorted with a stereomicroscope. Whole specimens and dissected material were mounted on slides in lactic acid for morphological inspection.

The terms 'furca' and 'telson' are used according to Schminke (1976). Terminology and homologization of maxillary and maxillipedal structures follow Ferrari and Ivanenko (2008). Therefore, by the application of serial homology, the nomenclature of Huys and Boxshall (1991) for Mx2 (Fig. 1.5.5, p. 26) is modified as follows: praecoxa of Mx2 is hereafter recognized as syncoxa (praecoxa and coxa), coxa is considered as the basis, and the basis is recognized as the first endopodal segment with claw. Drawings were made using an Olympus BX51 microscope equipped with a drawing tube, at a magnification of 400x and 1000x. Abbreviations: A1 (antennule); A2 (antenna); Md (mandible); Mxl (maxillula); Mx (maxilla); Mxp (maxilliped); enp (endopod); exp (exopod); benp (baseoendopod); P1 to P5 (legs 1 to 5); ap (apomorphy); pl (plesiomorphy); Urs (urosomite). The type material has been deposited in the invertebrate collection of the Museu de Zoologia da Universidade de São Paulo - MZUSP, São Paulo, Brazil. Specimens of both sexes were prepared for scanning electron microscopy (SEM) following protocols by Felgenhauer (1987), and Huys and Boxshall (1991).

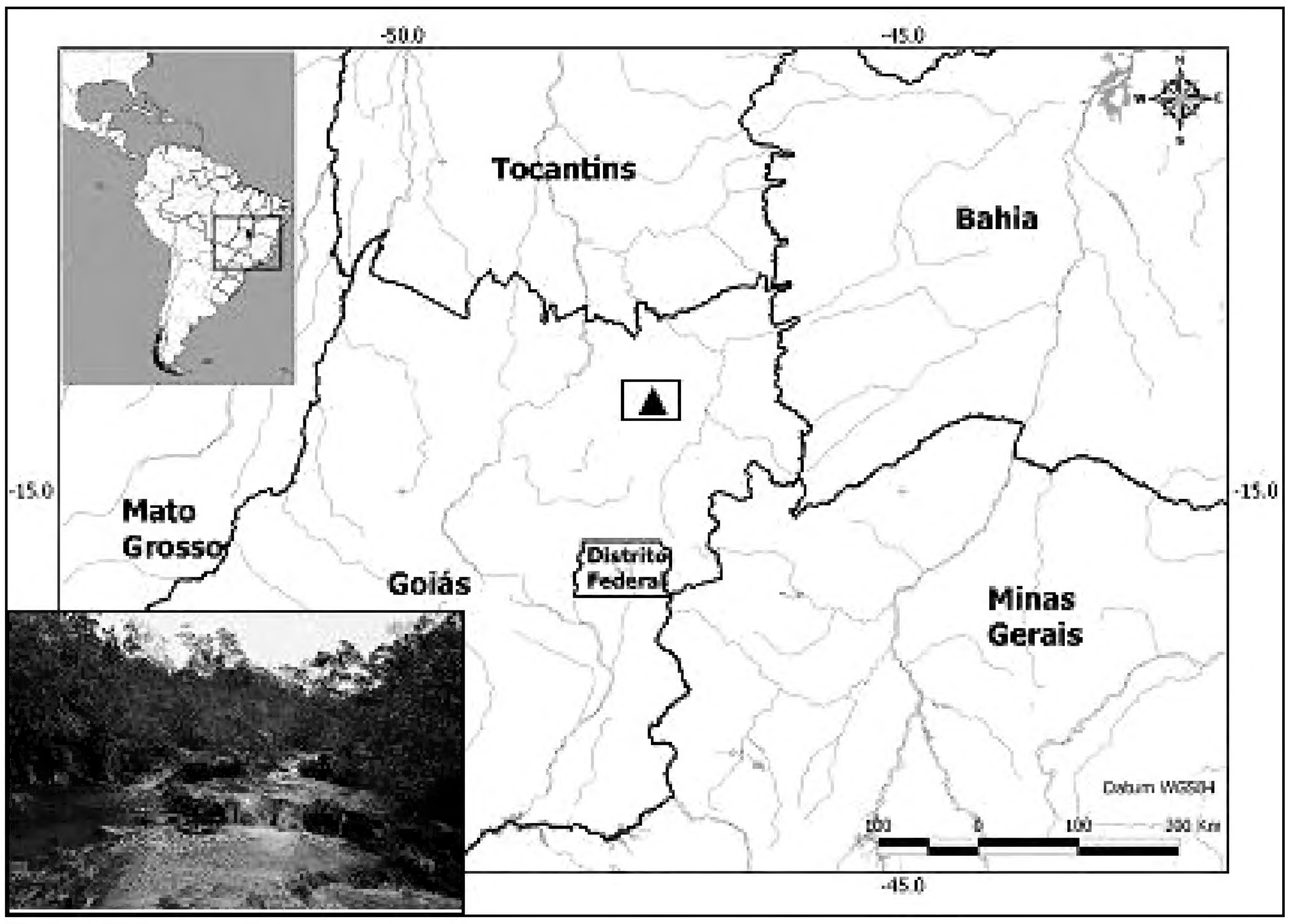

Figure 1. Study area. Type locality indicated with triangle. Insert shows the type locality (Água Fria River, National Park of the Chapada dos Veadeiros, Brazil) of *Eirinicaris antonioi* sp. n.

In order to determine the position of the new genus within Parastenocarididae, the method of phylogenetic systematics of Hennig (1966) was followed. The cladogram (Fig. 9) was generated using the program NONA (Goloboff 1999) for cladistic parsimony in interface with WINCLADA (Nixon 2002). This program uses a heuristic algorithm with unconstrained search and multiple TBR + TBR (searches for trees using tree bisection-reconnection method of branch-swapping, then repeats this process the number of times as indicated in the number of replications box) as search strategy for the best topology, and a Wagner algorithm that supports character reversal (allows $0 \rightarrow n$ and $n \rightarrow 0$ character changes) as a "similarity" algorithm. Character states are coded as binary (0-1) or multistate (0-n). We allowed the software to run characters as additive ($0 \leftrightarrow 1 \leftrightarrow 2 = 2$ steps; $0 \leftrightarrow 2 = 2$ steps). The state for each character can be seen in the character list. The data matrix is given in Table 1. The polarisation of characters was done a priori (zero (0) represents the plesiomorphic condition, one (1) the apomorphic condition, and one (1) is plesiomorphic in comparison with two (2)) as in the ground pattern characters for Parastenocarididae (Corgosinho et al. 2007a), Parastenocaridinae and Fontinalicaridinae (Schminke 2010). Additional decisions of character polarity were obtained by comparing the Parastenocarididae ground pattern with the state of character present in *Psammonitocrella* Rouch, 1992, and other Ameiridae. The resulting cladogram is rooted. The term "ground pattern" is used here in the sense of 'Grundmuster' (Ax 1984: 156) and refers to all plesiomorphies and autapomorphies present in each taxon ('Stammart' sensu Ax 1984). Uninformative characters were not mapped. Unsupported nodes in the tree are hard collapsed. Characters are ACCTRAN (fast) optimized.

The phylogenetic analysis is based on data from published literature. All the original descriptions and the descriptions of the species included in Lang's (1948) groups and Jakobi's (1972) genera of Parastenocaridinae were studied. The observation of the state of characters on outgroups and on the remaining species included within the Parastenocaridinae by Schminke (2010), which are not mentioned by Lang (1948) and Jakobi (1972), was possible by studying the drawings and descriptions present in a catalogue compiled by the first author.

When necessary in the text is used of the Newick (parenthetical) phylogenetic notation to discuss the species relationships within and between closely related clades.

Results

Subclass COPEPODA Milne-Edwards, 1840
Order HARPACTICOIDA Sars, 1903
Family PARASTENOCARIDIDAE Chappuis, 1940

Genus *Eirinicaris* gen. n.

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Diagnosis. A1 eight-segmented in male, seven-segmented in female. Male A1 haplocer, eight-segmented, haplocer, with small process in segment seven; segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bent inwards against segment 6, segment 8 points in opposite direction. Allobasis of Mx with two endites; proximal endite with one seta; distal endite with two elements, one of them transformed into serrated spine; proximal endopodal segment drawn out into claw, distal endopodal segment with two setae. Basis of P1 without remarkable sexual dimorphism; with inner and outer seta, the former longer in male; enp

Table 1. Character matrix for phylogenetic reconstruction of the valid genera included by Schminke (2010) within the subfamily Parastenocaridinae. Character states polarized a priori; polarization from 0= most plesiomorphic to 4 = most apomorphic. ?= unknown state of the character.

Ameiridae	1110000000	0000000000	0000000000	0000000000	0100000000	0000000000	0000000000	00000000
Fontinalicaris	0001211111	1111111111	1111111110	0000000000	0100000000	0000000000	0000000000	00000000
Remaneicaris	0001111111	1111111111	1110100001	1011100111	1010000000	0000000000	0000000000	00000000
Himalayacaris	0001211111	1111111111	1111100001	0112111000	0100000000	0000000000	0000000000	00000000
Indocaris	0001211111	1111111111	1110100001	1011100111	1003000000	0000000000	0000000000	00000000
Parastenocaris	0001211111	1111111111	1111100011	1110000000	0103111111	1111000000	0000000000	00000010
Kinnecaris	0001211111	1111111111	1111100001	1110000111	1101111110	0000110001	1100000000	00000110
Monodicaris	0001211111	1111111111	1111100001	1110000111	1102111110	0000110001	1010000000	00000?10
Macacocaris	0001211111	1111111111	1111100001	1110000000	0102100000	0000000001	0010012000	00000002
Simplicaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000013010	02010000
Asiacaris	0001211111	1111111111	1111000?1	1110000000	0106100000	0000000000	0000004000	10000000
Stammericaris	0001211111	1111111111	1111100011	1110000000	0102100000	0000000000	0001011000	00000001
Cottarellicaris	0001211111	1111111111	1111100011	1110000000	0102100000	0000000000	0001101000	00000002
Clujensicaris	0001211111	1111111111	1111100001	1110000000	0106100000	0000000000	0000014000	00100000
Entzicaris	0001211111	1111111111	1111000?1	1110000000	0101100000	0000000000	0000002211	00000000
Italicocaris	0001211111	1111111111	1111000?1	1110000000	0101100000	0100000000	0000002100	00000000
Michelicaris	0001211111	1111111111	1111100001	1110000000	0101100000	0000000000	0000000000	00000003
Minutacaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000013000	00100000
Nanacaris	0001211111	1111111111	1111100001	1110000000	0105100000	0000000010	0000014010	00000000
Eirinicaris	0001211111	1111111111	1111100001	1110000000	0104121000	0000111110	0000000000	00000121
Horstkutcaris	0001211111	1111111111	1111100001	1110000000	0104100000	0000000000	0000002211	00000000
Lacustricaris	0001211111	1111111111	1111100011	1110000000	0101100000	0000000000	0000012010	01011003

not sexually dimorphic. P2 enp without marked sexual dimorphism. Male P3 with quadratic smooth coxa; basis short, quadratic, with row of spinules close to outer seta, without inner ornamentation; enp modified, aesthetasc-like; exp unisegmented, rectangular, longer than wide, with irregular inner margin and with medial hump, outer margin straight, with unevenly distributed spinules, distal margin flat, inner apophysis shorter than supporting segment, blade-shaped, without distal seta or spine, thumb slightly longer than apophysis, with broad base, proximal expansion on both sides and leaf-shaped distal blade. Female P3 with spiniform enp ⅔ as long as exp-1. Male P4 enp cylindrical, approximately half as long as exp-1, with three distal spinules and one medial outer spinule. Enp of female P4 spiniform, almost as long as exp-1, distally bipinnate. Male and female P5 well developed, a simple triangular plate reaching middle of genital somite in male, inner margin drawn into long and pointed, outwardly curved, spinous process with distal pore, without inner ornamentation, reaching beyond the genital field in female; armature consisting of very long outer basal seta and two additional setae, of which proximal most shorter. Male P6 large, tetra-lobbed fused plate covering genital area. Female P6 represented by naked opercular plate much broader than the height covering genital opening. Male telson with proximal lateral pore, transverse row of small spinules along entire dorsal surface, anterior to sensilla, and rows of spinules covering most of preopercular lateral margin. Female telson smooth, with proximal ventral pore and ventral tube pore near insertion of furca. Male furca irregular, with distal outer pore, longer than width, inner and dorsal margins convex, outer and ventral margins concave; dorsal, inner and outer margins covered by spinules; lateral setae I, II and III, and dorsal setae VII separated by wide gap, setae I, II, and III displaced to antero-ventral position, seta I modified into short spine, with broad base and acuminate tip, seta III 1/3 as long as furca, with one long peduncle and one distal aesthetasc-like structure, 1/2 size of seta II, seta II with broad base, a long peduncle and one distal aesthetasc-like structure; setae IV to VII smooth, dorsal seta (VII) medially inserted in a depression; seta IV inserted subdistally on outer margin, approximately as long as telson without furca, seta V distal, twice as long as seta IV, seta VI distal, 1/2 as long as seta IV; proximal bulges on inner and outer margins. Female furca rectangular with distal ventral pore, longer than wide, smooth, slightly tapering distally, with inner flat lobe; setae smooth, lateral setae I, II, and III, and dorsal seta VII inserted medially and more or less opposite to each other; lateral setae reduced to one small (seta III) and two tiny setae (setae I and II); two uncinate processes anterior to insertion of dorsal seta VII, setae IV, V and VI inserted distally, length and ornamentation of setae IV, V, and VI as for the male; seta VI inserted beneath flat lobe, small spinules close to its insertion.

Eirinicaris antonioi gen. et. sp. n.

http://zoobank.org/8F621641-4E8D-4D91-825D-81734B42BCEC
Figs 2–8

Type material. Male dissected holotype mounted onto three slides (sample VEA17/B/R/ROF/musgo; 20 Jan 2012; MZUSP 35273). One dissected female paratype

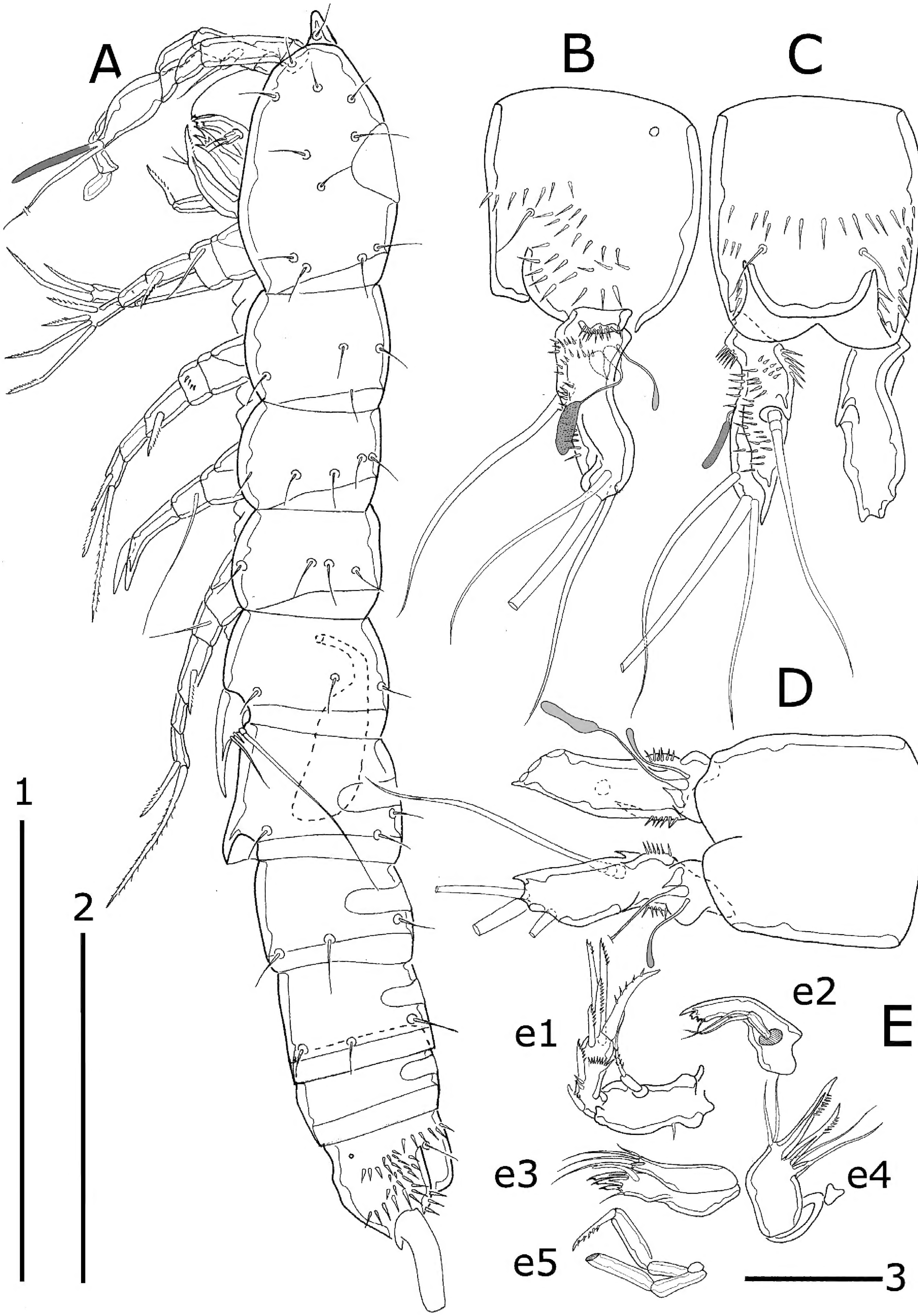

Figure 2. *Eirinicaris antonioi* sp. n. Male: **A** habitus, lateral view; **B** anal somite with caudal furca, lateral view; **C** anal somite with caudal furca, dorsal view; **D** anal somite with caudal furca, ventral view; **E** mouthparts; **e1** antennule; **e2** mandible; **e3** maxillulae; **e4** maxillae; **e5** maxilliped. Scale bars: **1** = 50 µm (**A**); **2 (B, C, D)** = 50 µm; **3 (E)** = 20 µm.

mounted onto one slide (sample VEA17/B/R/ROF/musgo; 20 Jan 2012; MZUSP 35274), one undissected female paratype (sample VEA15/C/CP/50; 20 Dec 2012; MZUSP 35274), and two undissected male paratypes mounted onto a single slide (sample VEA17/B/R/ROF/musgo; 20 January 2012; MZUSP 35274).

Type locality. National Park of the Chapada dos Veadeiros (North of Goiás, Brazil); Água Fria River; 1230 m MSL; speed of water current from low to medium; temperature 20 ±5°C; pH 5 ±1. Coordinates: 14°5'30.89"S, 47°29'34.47"W.

Etymology. The generic name is in honour of the first author's wife, Eirini Grapsa, combining her first name with the ancient Greek substantive for shrimp, καρίς (caris). The specific epithet "antonioi" is posthumous homage to Antonio Alves Corgosinho Filho, father of the first author.

Description of male. Length 320μm (variability of the type series 314-328μm), measured from rostrum to end of telson excluding furca. Rostrum not fused to cephalothorax, with wide base and two sensilla on tip (Fig. 2A). Cephalothorax and Urs-2-5 with dorsal integumental window (Fig. 2A). Patterns of sensilla as depicted. Telson with transverse row of small spinules dorsally, anterior to sensilla, and with rows of spinules covering most of preopercular lateral margin (Figs 2A, B, C), without ornamentation ventrally (Fig. 2D), posteriorly clefted, conferring a bilobate shape posteriorly (Fig. 6D), with a pore on the ventro-lateral margin. Furca irregular, with inner and outer bulges proximally (Figs 2B–D and 6D–F) with distal outer pore (Fig. 6F, arrowed), about three times as long as width, inner and dorsal margins convex, outer and ventral margins concave; with dorsal, inner and outer spinules; with seven setae as follows: setae I, II and III and dorsal seta VII not aligned, separated by wide gap; setae I, II and III displaced anteroventrally; seta I modified into short spine, with broad base and acuminate tip; seta II with broad base, a long peduncle and one distal aesthetasc-like structure, twice as long as seta III, the latter 1/3 as long as furca, with a long peduncle and one distal aesthetasc-like structure; setae IV to VII smooth; seta IV inserted subdistally on outer margin, about as long as telson excluding the furca; seta V inserted distally, twice as long as seta IV; seta VI inserted distally next to seta V, shorter than seta IV; dorsal seta VII inserted in a depression located in the middle of the furca.

A1 (Figs 3A, B; 6A, B) eight-segmented, haplocer, with small process in segment seven (arrowed on Figs 3A, B; 6B); segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bent inwards against segment 6, segment 8 points in opposite direction (Fig. 6B); segments armature as follows: 1 (0)/2(5)/3(4)/4(1)/5(3+ (1+ae))/6(0)/7(0)/8(7+ modified seta + (2+ ae)); segment 8 with seven slender setae, two seta fused basally to aesthetasc, and one modified seta, the latter as in Fig. 6C.

A2 (Fig. 2e1) allobasis without abexopodal armature, with small outer spinule proximally; one-segmented exp with one bipinnate seta; free endopodal segment bearing seven setae/spines, outermost strongly developed.

Labrum (not shown) triangular in lateral view.

Md as in Fig. 2e2. Coxal gnathobasis with distal teeth and one seta; palp one-segmented, with two distal setae.

Mx1 as in Fig. 2e3. Praecoxal arthrite with five elements (one surface seta, three claw-like pinnate spines, and one slender seta); coxal endite with one, basis with three setae.

Mx as in Fig. 2e4. Allobasis with two endites; proximal endite with one, distal endite with two elements, one of them transformed into serrated spine; proximal endopodal segment drawn out into claw, distal endopodal segment with two setae.

Mxp (Fig. 2e5) subchelate; syncoxa about 1/3 the length of basis; enp drawn into spinulose claw.

P1 (Figs 3B, 7A). Unarmed coxa ornamented with posterior row of spinules; inner seta of basis reaching tip of enp-1, with small row of spinules near insertion of enp, with comparatively smaller outer seta, with pore and row of spinules beneath outer seta; enp two-segmented, enp-1 nearly as long as exp-1 and exp-2 combined, with inner row of spinules (Fig. 7A), and two outer rows of spinules; enp-2 with one outer spine and one long geniculate seta, with posterior hyaline frill; exp three-segmented, exp-1 with outer spine, proximal and distal rows of spinules on outer margin, proximal and distal to outer spine, exp-2 unarmed, with row of inner spinules close to distal corner, exp-3 with outer row of spinules proximally, with two outer spines and two geniculate apical setae.

P2 (Figs 3C, 7A–B) coxa ornamented with posterior spinules; basis without outer seta, with row of spinules on outer margin and one outer pore; enp one-segmented, reaching middle of exp-1, armed with one distal seta, ornamented with one distal and two outer spinules; exp three-segmented, exp-1 with long outer spine, ornamented with medial row of outer spinules, with one long spinule and smaller spinule close to outer spine (Figs 3C, 7B), with hyaline inner frill; exp-2 unarmed, with distal row of spinules; exp-3 with one outer unipinnate spine, one distal unipinnate spine twice as long as outer element, and one bipinnate apical seta nearly twice as long as previous element, additionally with longitudinal row of spinules on distal third, proximal to outer spine and inner hyaline frill.

P3 as in Figs 3D, d1, d2 and 7B-C. Coxa quadratic, with posterior row of spinules; basis short, quadratic, with outer pore, with row of strong spinules close to exp; enp modified as claviform aesthetasc-like seta (Figs 3D, 7B–C); exp unisegmented, rectangular, about four times as long as wide, inner margin irregular, with one medial inner hump, outer margin straight, with unevenly distributed spinules, distal margin flat, inner apophysis shorter than exp, blade-shaped, without distal spine or seta, completely fused to exp, thumb slightly longer than apophysis, blade-shape, with broad base, curved inwards proximally.

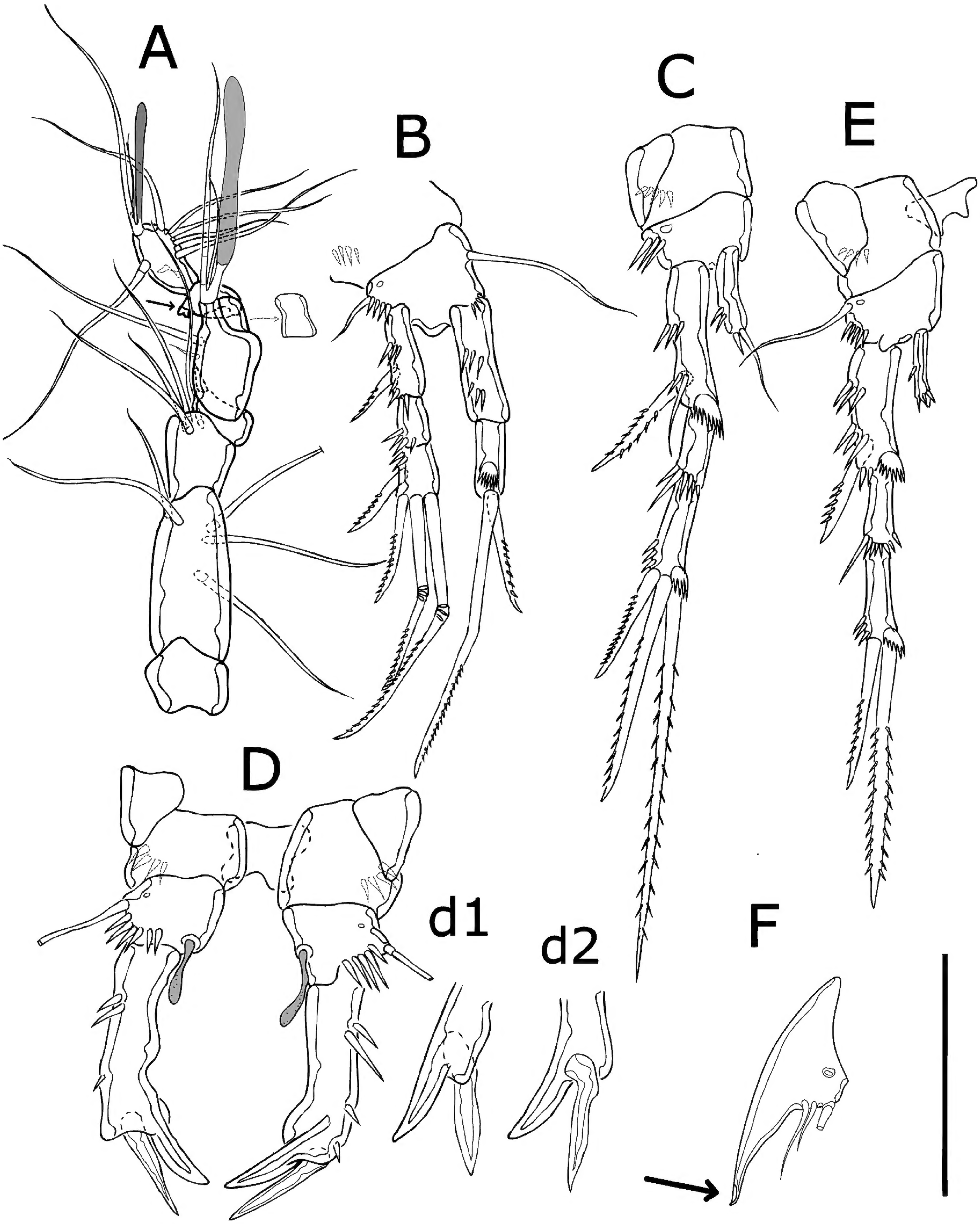

Figure 3. *Eirinicaris antonioi* sp. n. Male: **A** antennule, with process arrowed on segment seven, segment six laterally detached; **B** P1, anterior; **C** P2, anterior; **D** P3, anterior; **d1** distal part of exopod of P3 showing the apophysis, anterior; **d2** distal part of exopod of P3 showing the apophysis, posterior; **E** P4, anterior; **F** P5, with distal pore arrowed. Scale bar = 25µm.

P4 as in Figs 3E, 7B. Coxa with posterior row of spinules; basis with outer pore, outer seta, and row of outer spinules close to exp; enp cylindrical, with accuminate tip, approximately half the length of exp-1, with three distal spinules and one medial outer spinule; exp 3-segmented, exp-1 with long outer spine, ornamented with row of spinules proximally and subdistally, with comparatively smaller distal spinules, and inner hyaline frill; exp-2 un-

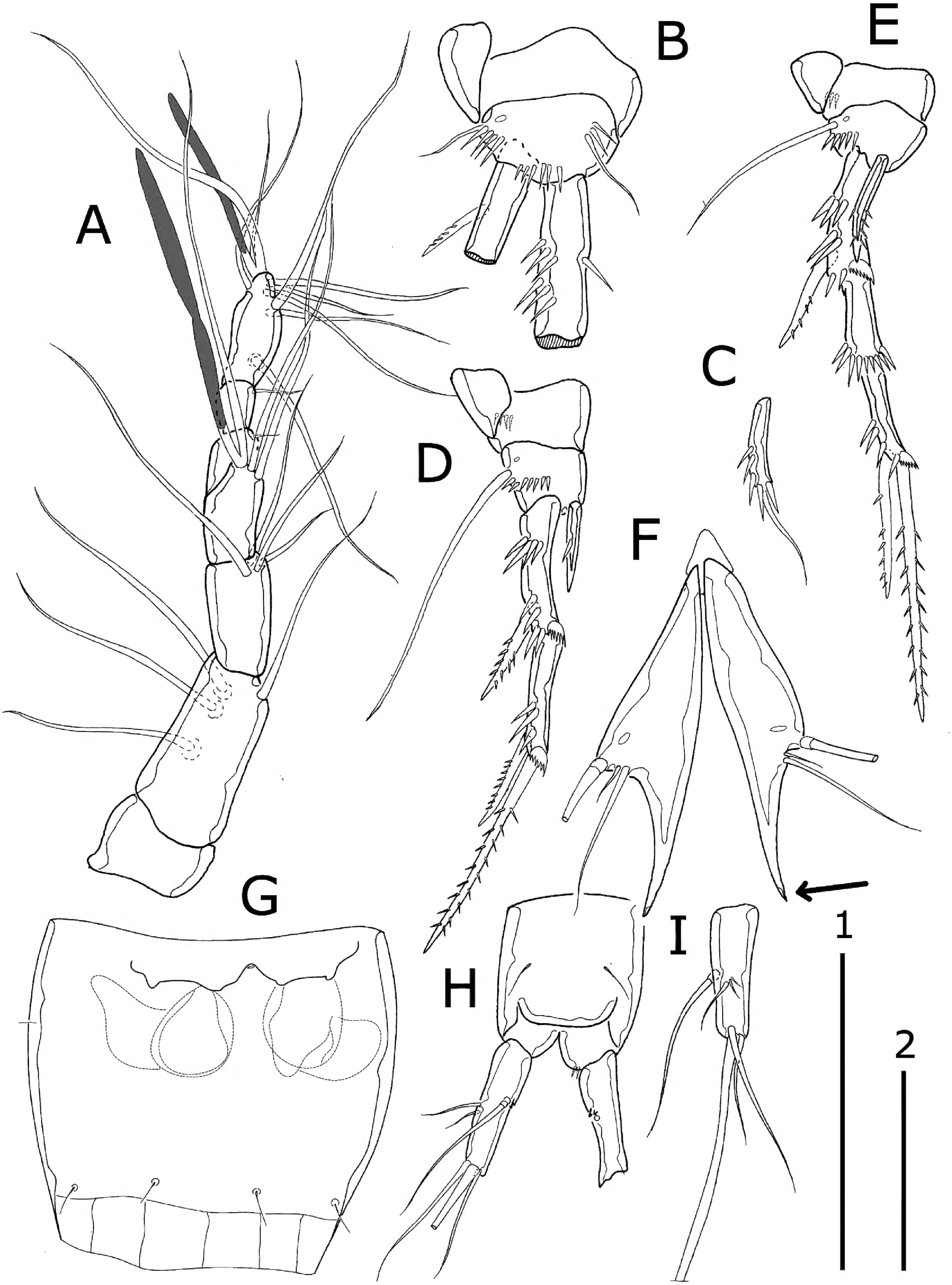

Figure 4. *Eirinicaris antonioi* sp. n. Female: **A** antennule; **B** P1, depicted with coxa, basis enp-1 and exp-1; **C** P2 enp; **D** P3, anterior; **E** P4 anterior; **F** P5, with distal pore arrowed; **G** genital field; **H** anal somite with caudal furca; **I** furca, lateral view. Scale bar 1 (**A, F**) and 2 (**C, D, E, G, H, I**) = 25µm.

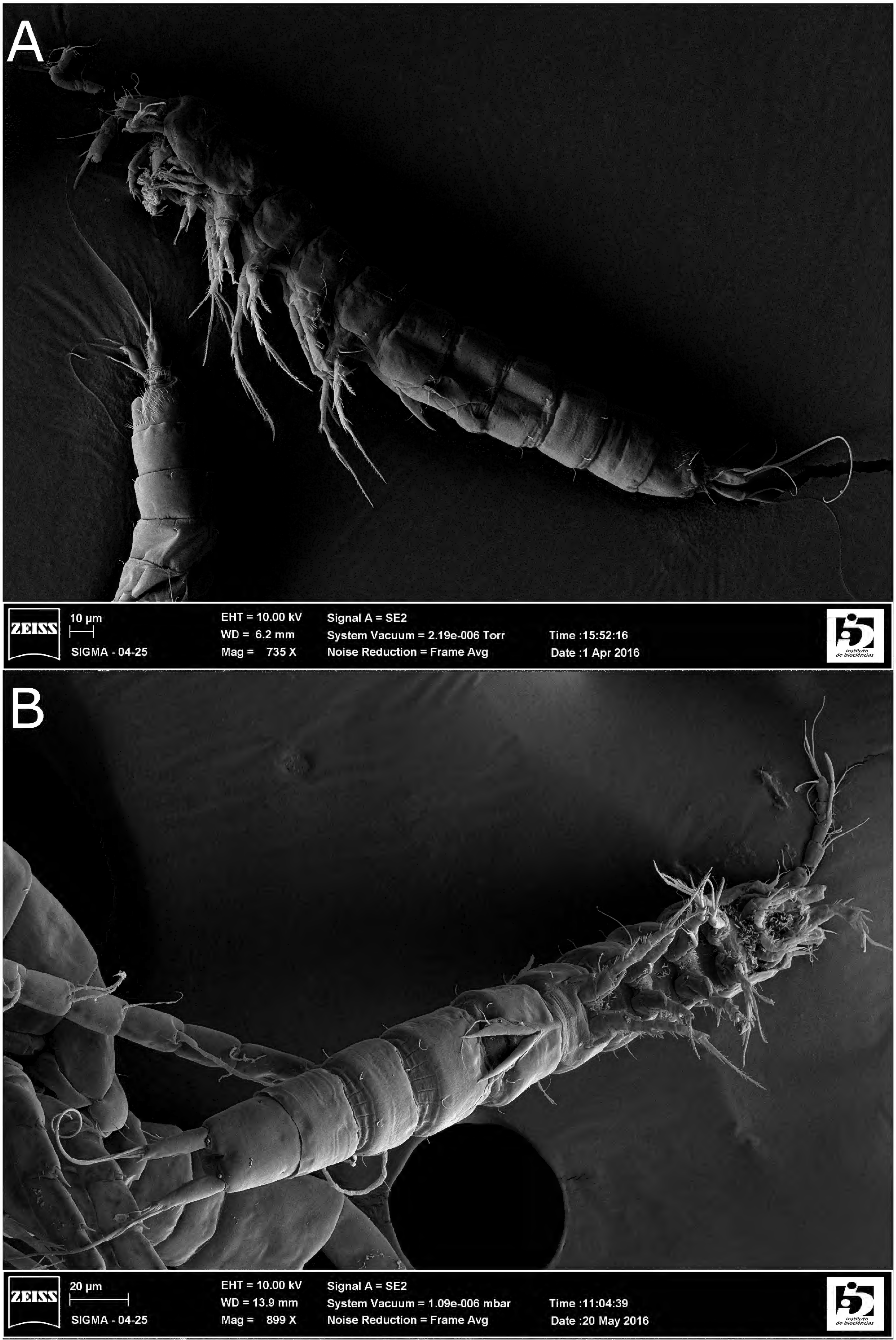

Figure 5. SEM image of *Eirinicaris antonioi* sp. n. **A** male habitus, lateral view; **B** female habitus, ventral view. Scale bar **A** = 10µm; **B** = 20µm.

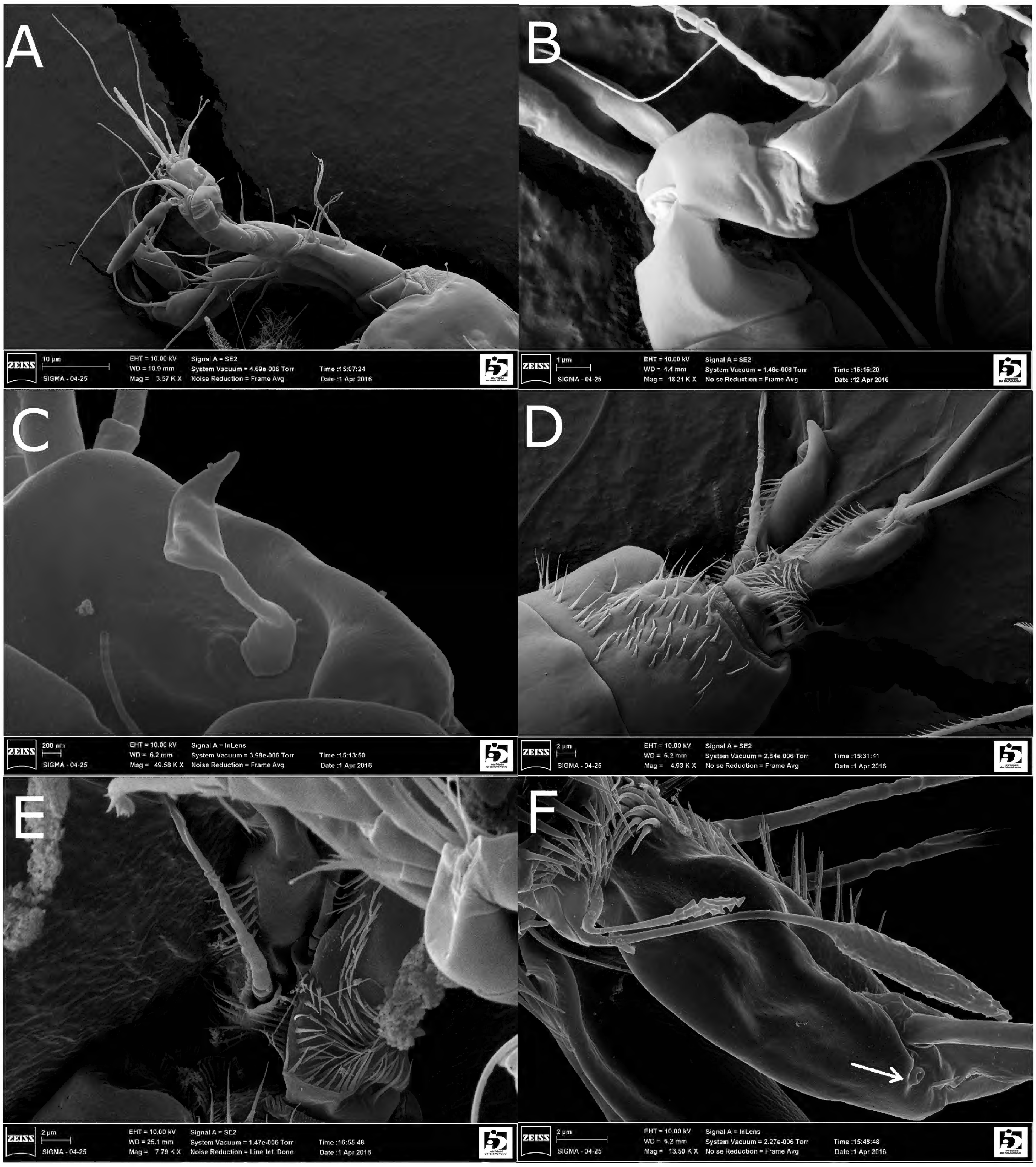

Figure 6. SEM image of *Eirinicaris antonioi* sp. n. Male: **A** antennule in lateral view; **B** antennule segments 6 (yellow) and 7 (coral); **C** antennule, segment 8 showing modified seta; **D** telson and furca, lateral; **E** furca, dorsal view; **F** furca, ventral view, showing modified setae I, II and III and distal pore arrowed. Scale bars **A** = 10µm; **B** = 1µm; **C** = 200µm; **D** = 2µm; **E** = 2µm; **F** = 2µm.

armed, with distal row of spinules (a long one on outer edge; arrowed), exp-3 with row of outer spinules subdistally, with one unipinnate outer spine, and one bipinnate distal seta nearly twice as long as outer element.

P5 (Figs 3F, 7D–E) well developed reaching slightly beyond middle of second urosomite; simple triangular plate with outer pore, distal inner margin a long and pointed, outwardly curved, spinous process with distal pore (arrowed on Figs 3F and 7D), without inner ornamentation; armature consisting of very long outer basal seta and two shorter elements, of which proximal one shortest.

P6 (Fig. 7E), large tetra-lobbed fused plate covering genital area.

Description of female. Length 310µm (variability of the type series 310-326µm), measured from tip of rostrum to end of telson, excluding furca. Sexual dimorphism ex-

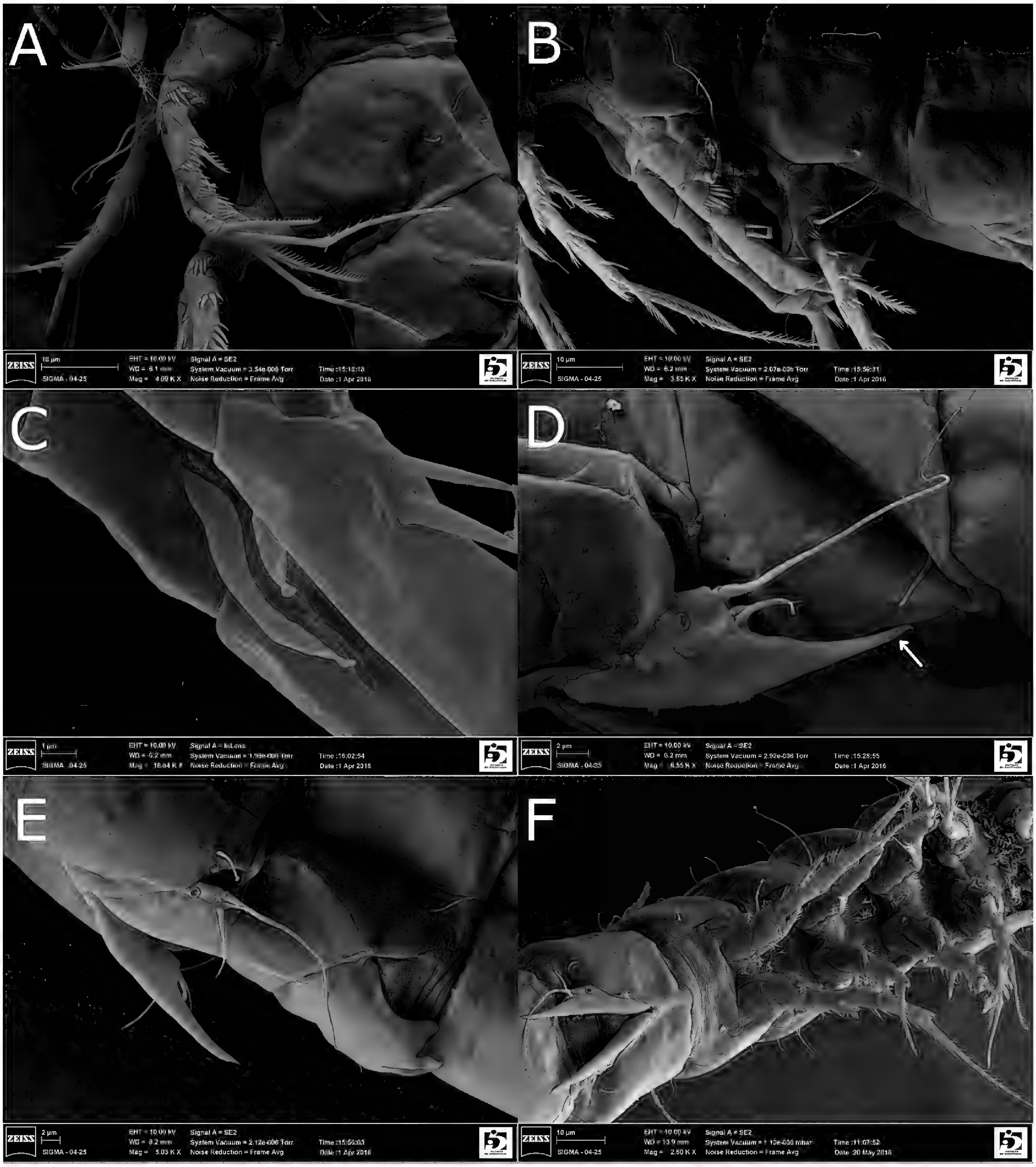

Figure 7. SEM image of *Eirinicaris antonioi* sp. n. Male: **A** P1 showing inner seta of basis; **B** P3 with endopod and thumb in colour, P4; **C** claviform aesthetasc representing the endopod of P3; **D** P5, lateral view, with distal pore arrowed; **E** P5 and P6. Female: **F** pro- and urosomites, ventral view showing endopods of P3 and P4, and P5 and P6. Scale bars **A** = 10μm; **B** = 10μm; **C** = 1μm; **D** = 2μm; **E** = 2μm; **F** = 102μm.

pressed in A1, P1, P3, P4, genital-double somite, number of integumental windows, telson and furca. Cephalothorax and Urs-2-4 with dorsal integumental windows; window on Urs-4 extending into ventral area (Figs 5B, 8A-B). Telson smooth, and small ventral tube pore near insertion of furca (Fig. 8A, arrowed); anal operculum smooth and convex (Figs 4H, 8B). Furca (Figs 4H-I, 5B, 8A-B) rectangular, with distal ventral pore (Fig. 8A, arrowed), three times as long as wide, smooth, slightly tapering distally, with seven smooth setae as follows: setae I, II and III, and dorsal seta VII inserted medially, aligned, the former three setae more or less opposite to the latter; lateral setae reduced to one small (seta I) and two tiny setae (seta II and III); with two uncinate processes anterior to insertion of dorsal seta (Fig. 4H, arrowed), setae IV, V and VI inserted distally, length and ornamentation of setae IV, V, VI, and VII as in male.

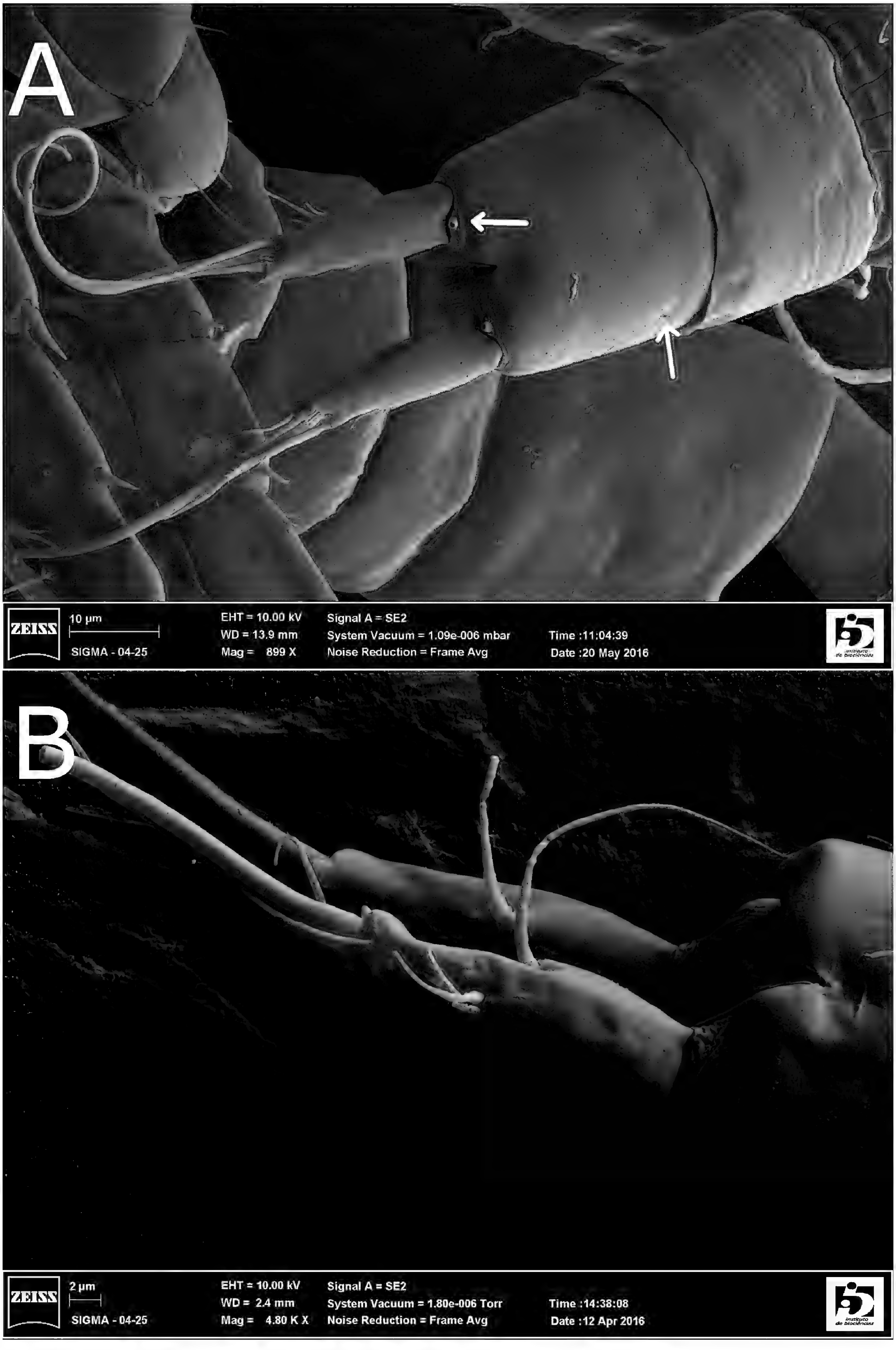

Figure 8. *Eirinicaris antonioi* sp. n. Female: **A** last urosomite, telson and furca, ventral view, proximal and distal pores arrowed; **B** telson and furca, lateral view. Scale bars **A** = 2µm; **B** = 10µm.

A1 seven-segmented (Figs 4A, 5B); armature as follows: 1(0)/2(4)/3(4)/4(2+ (1+ae))/5(1)/6(1)/7(7+ (2+ae)).

P1 (Fig. 4B) as in male, with comparatively shorter inner basal seta.

P2 enp (Fig. 4C), slightly dimorphic in ornamentation, with three outer and 2 distal spinules; exp three-segmented, exp-1 without long outer spinule close to the insertion of the outer spine.

P3 as in Figs 4D, 7F. Coxa with posterior row of spinules; basis with outer pore and row of spinules close to outer seta, the latter long; exp two-segmented, exp-1 with proximal row of spinules, outer spine, row of spinules around outer spine, and inner hyaline frill; exp-2 with subdistal row of outer spinules, with inner hyaline frill, outer unipinnate spine and distal bipinnate element; enp one-segmented, spiniform, with one outer spinule as shown, ⅔ the length of exp-1.

P4 (Figs 4E, 7F) coxa and basis as in male; exp-1and 3 as in male, enp-2 without long spinule on outer edge; enp (Fig. 4E) spiniform, about as long as exp-1, distally bipinnate.

P5 (Figs 4F, 5B, 7F) well developed, a simple triangular plate; distal margin a long and pointed, outwardly curved, spinous process with distal pore (Fig. 7F, arrowed), without inner ornamentation, reaching beyond genital field; armature as in male.

P6 (Figs 4G, 7F) represented by naked opercular plate much broader than height covering genital opening.

Discussion

After the revisionary work of Jakobi (1972), attempts to resolve the taxonomy and phylogenetic systematics within the Parastenocarididae resulted in the proposition of two subfamilies (Schminke, 2010), some new genera, and the redefinition of some other taxa (Table 2). However, some questions remain unanswered and the taxonomic and phylogenetic relationships within the family are far from complete.

Of the genera mentioned on Table 2, only *Simplicaris*, *Monodicaris*, *Asiacaris, Parastenocaris, Remaneicaris*, *Kinnecaris*, *Stammericaris*, *Cottarellicaris, Himalayacaris* and *Indocaris* belong to the Parastenocaridinae. Schminke (2010) also included the following genera within this subfamily: *Clujensicaris*, *Entzicaris*, *Italicocaris*, *Macacocaris*, *Michelicaris*, *Minutacaris*, and *Nanacaris*. Karanovic et al. (2012) synonymised *Lacustricaris* with *Parastenocaris*. However, following Schminke (2013), such course of action was premature since the type species of *Lacustricaris* is not *Proserpinicaris lacustris* (Chappuis, 1958) but *Lacustricaris budapestiensis* (Toeroek, 1935). Therefore, the genus *Lacustricaris* must be reinstated in the future.

The genus *Eirinicaris* strongly differs from all the above Parastenocaridinae genera by its unique sexually dimorphic telson and furca. *Eirinicaris* does not exhibit all the diagnostic characters of Parastenocaridinae, as proposed by Schminke (2010) and its phylogenetic position within this subfamily is discussed below.

List of characters and phylogenetic discussion. The characters are listed below and the state of each character is indicated within parentheses.

1. Inner spine on the basis of leg 1: sexually monomorphic (0); sexually dimorphic (1);
2. Seta on the distal endite of Mx: modified, brush-like (1); not modified (0);
3. Seta on the Md palp: modified, brush-like (1); unmodified (0);
4. No. of armature elements on praecoxal arthrite of Mxl: >5 (0); 5 (1);
5. No. of segments of male A1: 10 (0); 9 (1); 8 (2);
6. No. of segments of female A1: 8 (0); 7 (1);
7. No. of segments of the A2 enp: 2 (0); 1 (1);
8. No. of armature elements on triangular A2 exp: three spines/setae, at least 1 modified (0); 1 seta (1);
9. No. of segments on mandibular palp: 2 (0); 1 (1);
10. Accessory setae on the first enp/claw of Mx: present (0); absent (1);
11. Syncoxal seta of Mxp: present (0); absent (1);
12. P4: sexually dimorphic (1); monomorphic (0);
13. No. of endopodal segments of P1: 3 (0); 2 (1);
14. Inner seta on enp-1 of P1: present (0); absent (1);

Table 2. List of genera redefined after Jakobi (1972) followed by the respective synonyms and genera proposed after Jakobi (1972).

Genera redefined after Jakobi (1972) and synonyms	*Parastenocaris* (sensu Reid 1995 and Karanovic and Lee 2012a partim.; Junior synonym: *Biwaecaris*; *Brinckicaris*, *Enckellicaris*, *Oshimaensicaris*), *Remaneicaris* (Corgosinho and Martínez Arbizu 2005), *Kinnecaris* (Schminke 2008; Junior synonym: *Cafferocaris*), *Brasilibathynellocaris* (Corgosinho et al. 2010a; Junior synonyms *Paraforficatocaris*, *Pararemaneicaris*), *Siolicaris* (Corgosinho et al. 2012b), *Proserpinicaris* (Karanovic et al. 2012; Juinior synonyms *Nipponicaris*, *Pannonicaris*) and *Stammericaris* (Schminke 2013; Junior synonym *Phreaticaris*)
New genera proposed after Jakobi (1972)	*Potamocaris*, *Murunducaris*, *Simplicaris* Galassi and De Laurentiis, 2004, *Monodicaris*, *Asiacaris*, *Dussartstenocaris*, *Horstkurtcaris*, *Iticocaris*, *Cottarellicaris*; *Himalayacaris* and *Indocaris*.

15. No. of endopodal segments of P2: 2 (0); 1 (0);
16. Exp-2 of P2: with outer seta (0); without (1);
17. Exp-2 of P2: with inner seta (0); without (1);
18. No. of endopodal segments of P3: 2 (0); 1 (1);
19. Exp-2 of P4: with outer seta (0); without (1);
20. Exp-2 of P4: with inner seta (0); without (1);
21. No. of endopodal segments of P4: 2 (0); 1 (1);
22. Exp of male P3: not prehensile (0); prehensile (1);
23. Integumental windows: absent (0); present on Cphl and urosomites (1);
24. Armature of the first Mx endite: 2 (0); 1 (1);
25. P5 exp and benp: separate (0); fused (1);
26. Inner seta on the basis of P1: present (0); absent (1);
27. Ornamentation of basis of the male P4 between exp and enp: present (1); absent (0);
28. Shape of the genital operculum: broader than height (0); higher than width (1);
29. Exp of the male P3: with a proximal hump (1), without hump (0);
30. Length and shape of enp of female P3: short and rounded (0); long and spiniform (1);
31. Relative position of lateral setae I, II and III, and dorsal furcal setae VII: aligned (1); dorsal seta posterior to lateral setae (0);
32. Penultimate segment of the male A1: with apophysis (1); without apophysis (0);
33. Armature of the apophysis of male P3: with one distal spine (0); spine lost or reduced to a hyaline structure (1);
34. No. of armature elements on second endite of Mx: two setae and one spine (0); 3 (1); 2 (2);
35. P5 intercoxal sclerite: present (0); absent (1);
36. Enp of the male P4 fused to the basis: present (1); absent (0);
37. Flat strong spine on coxa of male P4: absent (0); present (1);
38. Medial ornamentation on the outer margin of P4 exp-3: absent (0); present (1);
39. Medial ornamentation on the outer margin of P4 exp-2: absent (0); present (1);
40. Medial ornamentation on the outer margin of P2 exp-3: absent (0); present (1);
41. Medial ornamentation on the outer margin of P2 exp-2: absent (0); present (1);
42. Enp of male P3: present (0); absent or reduced to a seta (1);
43. Position of outer setae of P4 exp-3: distal (0); subdistal (1);
44. Ornamentation of the basis of the male P4: simple row of spinules (0); with normal spinules of equal sizes (1); sclerotized, of different sizes (2); with strongly transformed spinules building a spinular complex or differently build into petaloid structures (3); lost but conserving the enp (4); loss of enp (5) loss of ornamentation and enp (6);
45. Length of the apophysis of the male P3: short (0); long (1);
46. Relative position of male setae I, II and III, and dorsal furcal setae VII: setae I, II, and III and seta VII inserted at distal third of the furca, or setae I, II and III anterior to the dorsal seta VII (0); at the same plane on furca's midlength (1); setae I, II and III located proximally in the ventral margin of the furca, dorsal seta VII on the distal third (2);
47. Relative position of female lateral and dorsal furcal setae: lateral and dorsal seta inserted at the distal 1/3 of the furca or setae I, II, and III are anterior to the dorsal seta VII (0); at the same plane on furca's midlength (1);
48. Shape of female furca: cylindrical (0); tapering distally (1);
49. Hyaline margin of male P3: present (1); absent (0);
50. Sexual dimorphism on P5: strong, based on difference of length (1); absent or based on differences of ornamentation (0);
51. Width of the proximal part of the endopod of male P4: narrow base (0); broad base (1);
52. Length and ornamentation of the endopod of the female P4: longer than exp-1with ornamentation at distal 1/3; shorter than exp-1 or as long as exp-1 (0);
53. Shape of exp-1 of the male P4: strongly concave at the inner margin (1); not concave (0);
54. Shape of exp of the male P3: inflate, with proximal and medial hyaline cushions (1); without this character (0);
55. Length of male P5: spiniform process reaching far beyond its own urosomite (1); short (0);
56. Length of female P5: spiniform process reaching far beyond its own urosomite (1); short (0);
57. Furca: dimorphic (1); monomorphic;
58. Enp of male P3: transformed into an aesthetasc-like seta (1); without this character (0);
59. Cuticle ornamentation of body somites: smooth (0); pitted (1);
60. Position of integumental window in the last and penultimate Urs: dorsal (0); lateral (1);
61. Size and shape of the inner process on the penultimate segment of the male A1: strong and sickle-shaped (1); different shape (0);
62. Ventral ornamentation of male Urs 3: two groups of spinules (1); absent (0);
63. Size of enp of the male P2: normally developed (0); strongly reduced (1);
64. Shape of the enp of the male P4: "Y"-shaped, proximally bifurcate, with a distal flagellum or lamella (1); of a different shape;
65. Shape of the apophysis of the male P3: foliaceous and acuminate (1); different (0);
66. Length of the thumb of the exopod of the male P3: longer or as long as apophysis (0), shorter than apophysis (1);
67. Shape of the enp of the male P4: foliaceous or triangular lamella (0); y-shaped enp (1); long spiniform (2); short, claw-like, outwardly curved (3); lost (4);

68. Shape of the apophysis on the male P3 exp: smooth (0); proximally dilated, with a soft median attenuation and a thinner distal lamella at the outer margin (1); proximally dilated, with a subtle median depression and a thinner distal lamella (2);
69. Length of furca relative to the telson: longer than telson (1); as long or shorter than telson (0);
70. Shape of the enp of the male P4: spiniform, curved inwards, sigmoid (1); different shape (0);
71. Enp of the male P2: present (0); absent (1);
72. P5 in both sexes: present (0); reduced (1); absent (2);
73. Shape of thumb of the exp of the male P3: a pointed spine (0); digitiform, with rounded tip (1);
74. Outer seta of basis of P4: present (0); absent (1);
75. P5 dimorphism: with a single seta in both sexes, elongate in male (1); with 2 or more setae (0);
76. Distal pore on the spiniform inner process of P5: present (1); absent (0);
77. Shape of male furca: cylindrical (0); tapering distally (1); allometric in growth (2);
78. Ornamentation of the proximal outer margin of the male P3: more than two spinules (0); two spinules (1); less than two spinules (2); not ornamented (3);

The phylogenetic study of the family Parastenocarididae is a difficult task, which means working up Jakobi's (1972 a, b) legacy (Schminke 2013). The family is notorious for its ill-defined genera (Galassi and De Laurentiis 2004), and researchers must deal with a plethora of poorly detailed descriptions, a high level of convergence, and ample distribution of plesiomorphic characters between and within groups and genera, making generic divisions difficult (Reid 1995, Galassi and De Laurentiis 2004, Karanovic 2005, Schminke 2010, Corgosinho et al. 2012a, b, Karanovic and Lee 2012a, b).

A phylogenetic hypothesis of the evolution of the subfamily Parastenocaridinae is herein proposed in order to discuss the phylogenetic position of the genus *Eirinicaris*. Recently, Schminke (2013) showed that meaningful conclusions could be drawn from available data. Meta-analysis of data collected from existing descriptions resulted in a single most parsimonious tree, with tree length, consistency index and retention index indicating a high level of convergence of characters within this subfamily (L=146, CI=68, RI=72) (Fig. 9).

The monophyletic status of the Parastenocarididae, Parastenocaridinae and Fontinalicaridinae were discussed in previous studies (Martínez Arbizu and Moura 1994; Schminke 2010; Ranga Reddy et al. 2014). Characters 1-29 are compiled from the contributions mentioned above. For polarization of these characters we recommend the studies of Martínez Arbizu and Moura (1994) and Ranga Reddy et al. (2014). The diagnostic characters for Parastenocaridinae and Fontinalicaridinae are proposed and discussed by Schminke (2010).

Parastenocaridinae. Schmincke (2010) proposes the following diagnostic characters for the Parastenocaridinae, avoiding to make inferences about the polarization of the characters: 1) the segments 5 and 7 form a functional unit for clasping the female. The segment 7 is sickle-shaped in some species, with an apophysis developed at the distal inner corner, and can fold back onto the fifth segment during copula whereas the segment 8 points medially; 2) female P3 enp is long and spiniform; 3) the apophysis of male P3 is unarmed in most of the species; 4) the coxa of male P4 lacks an inner row of spinules, but a row of spinules may be present near the insertion of endopod or medially of the basis; 5) except for species of *Kinnecaris*, *Monodicaris* and *Macacocaris*, all Parastenocaridinae share a small P5 in both sexes, not reaching far beyond its own somite; 6) female genital field is rectangular and much broader than high, and 7) the lateral setae I, II, and III occur at the same level as, and almost opposite to, the dorsal seta VII.

Eirinicaris can be included within the Parastenocaridinae because of the following synapomorphies (Characters 30–33):

a) Female P3 enp long, and spiniform, without distal seta (ap);
b) the group of three lateral setae of the furca (setae I, II and III), and the dorsal seta VII aligned (viz. female) (ap);
c) A1 is haplocer, with small process in segment 7 (this process is sickle-shaped in genera such as *Kinnecaris* and *Monodicaris*); segments 5, 6, and 7 forming a functional unit for clasping the female, in grasping position, segment 7 bends inwards against segment 6, segment 8 points in opposite direction (ap);
d) the apophysis and terminal seta of the exp of male P3 fused (ap);

In addition, *Eirinicaris* share the following symplesiomorphies with other Parastenocaridinae (Characters 26 and 28):

d) genital field rectangular, much broader than the height (pl);
e) basis of P1 with an inner seta (pl);

Length and shape of enp of female P3 (Character 30). Ranga Reddy et al. (2014) considered the female P3 with a terminal seta fused to the enp as a plesiomorphy for the Parastenocaridinae. However, we consider this character as an autapomorphy for the Parastenocaridinae, and the reduced, unarmed and linguiform enp as a plesiomorphy for the Fontinalicaridinae. Our decision is based on the observation of the copepodid development of the fontinalicaridin *Proserpinicaris phyllura* (Kiefer, 1938) described by Glatzel (1991). On both male and female copepodid IV the P3 enp is a linguiform structure, very similar to the adult. Hence, we consider the spiniform female P3 enp of Parastenocaridinae an autapomorphy.

Relative position of lateral and dorsal furcal setae (Character 31). This character is the best documented for the

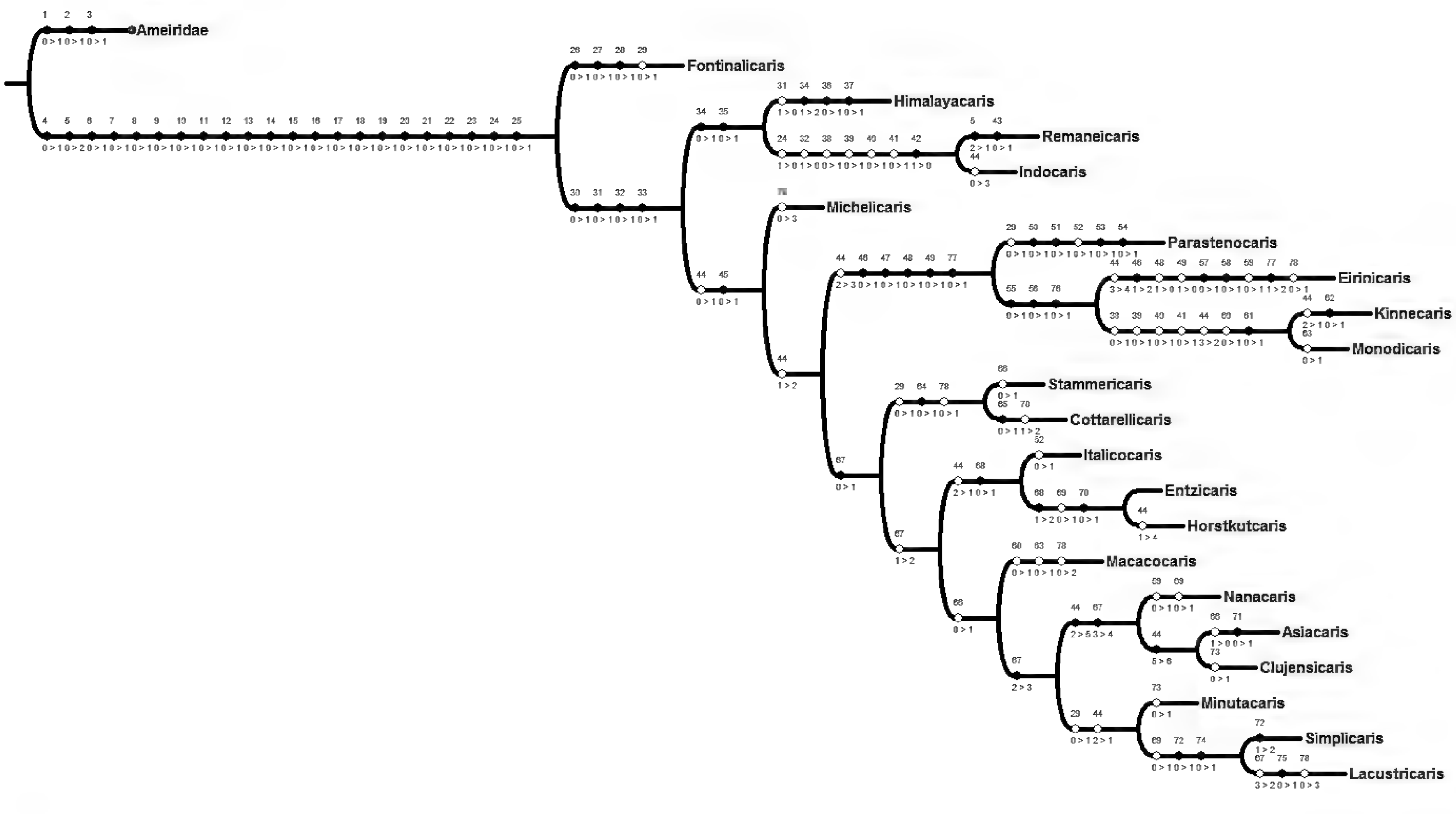

Figure 9. Phylogeny of the Parastenocaridinae reconstructed by applying Hennigian principles and criterion of putative parsimony based on the data matrix of Table 1. The cladogram was generated using the program NONA (Goloboff 1999) for cladistic parsimony, and in interface with WINCLADA (Nixon 2002). For details see Material and Methods. Characters as explained in the text; binary or multistate, polarized a priori; length of cladogram = 146. Circles represent autapomorphies, open circles represent autapomorphies by reversion of character state. Direction of character transformation indicated below each character.

family (Schminke 2010). There are three exceptions only in which the dorsal seta VII and the lateral setae I, II and III are not aligned. There is a slight gap between the lateral setae (setae I, II and III) and dorsal seta VII in *Remaneicaris euniceae* Corgosinho & Martínez Arbizu, 2005, and *Parastenocaris trichelata* Reid, 1995 (Schminke 2010). The lateral setae I, II and III are inserted at the middle of the furca, and the dorsal seta VII is inserted distally in *Himalayacaris alaknanda* Ranga Reddy, Totakura & Corgosinho, 2014. The anterior position of setae I, II and III, and the posterior situation of the dorsal seta VII is the condition described by Schminke (2010) for Fontinalicaridinae. This is a plesiomorphic condition also present in other Harpacticoida families such as Ameiridae Boeck, 1865, Cletodidae Scott T., 1904, Canthocamptidae Braddy, 1880, etc. With exception of *Eirinicaris* gen. n. and *Macacocaris*, the Parastenocaridinae condition, with lateral setae I, II and III, and dorsal seta VII aligned, and more or less opposite to each other, is observed in both male and female of those species for which both genders are described. In *Eirinicaris*, however, due to an allometric growth in the male, the lateral setae I, II and III are located proximally on the ventral margin, and the dorsal seta VII is inserted medially inside a depression, The normal condition for the subfamily is evident in the female of *Eirinicaris*. It has been suggested that the male and female of *Macacocaris* do not belong to the same species (Schminke 2009), given the presence of a parastenocaridin-like furca in the male, but a fontinalicaridin furca in the female. Although this is unusual, the sexually dimorphic furca observed for *Eirinicaris* proves that such dimorphism is possible.

Penultimate segment of the male A1 (Character 32), and geniculation. Similarly to other Parastenocaridinae with penultimate segment of the male A1 sickle-shaped, and with a functional clasping unit formed by segments 5, 6 and 7 (pocket-knife type, Schminke (2010)) as in *Kinnecaris* and *Monodicaris*, the functional unit for clasping is formed by the segments 5, 6 and 7 in *Eirinicaris* In both cases the terminal segment 8 of the male A1 points medially (ap). Galassi and De Laurentiis (2004) briefly addressed the different morphologies of the penultimate segment of the male A1 within the family Parastenocarididae. The study of the morphology of this segment in the Parastenocaridinae reveals some diverging morphologies. For example, in *P. brevipes* and many species of the genus *Parastenocaris* (sensu Reid 1995), the penultimate segment is strongly curved inwards, assuming a *quasi* horizontal conformation, conferring to the limb an appearance described as pocket-knife-like by Schminke (2010) and the last segment inserts subdistally or medially on the outer margin. Segment 7 has a medio-distal protrusion prolonged into a long process with rounded tip in *Simplicaris* (Galassi and De Laurentiis 2004: 420, Fig. 1C). However, segment 7 is aligned with the previous segment, and segment 8 inserts distally on segment 7, with the apophysis of the latter oriented obliquely to

segment 8 when the A1 is in resting position. This is considered here a modification of the sickle-shaped segment 7 as described by Schminke (2010) for the parastenocaridin pocket-knife male antennule. The morphology of the penultimate male A1 segment of *Simplicaris veneris* (Cottarelli and Maiolini, 1980) is similar to *Parastenocaris brevipes*. Nothing can be said about the shape and strength of this the male antennular apophysis for the type species of the genera *Michelicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris, Nanacaris*, *Clujensicaris*, *Minutacaris* and *Lacustricaris*. The male A1 apophysis is present in *Parastenocaris*, *Kinnecaris*, *Monodicaris*, *Eirinicaris*, *Stammericaris*, and *Cottarellicaris*. The presence in *Macacocaris* is questionable and open to interpretation since Chappuis (1952) only made reference to the presence of a strongly prehensile male A1. Following Galassi and De Laurentiis (2004), the transformation of the penultimate segment of the male antennule may have appeared independently within the family Parastenocarididae and should be considered a derived state. Instead, we consider the modifications of the 5th and 7th segment of the male A1 as synapomorphies for the Parastenocaridinae (Ranga Reddy et al. 2014). However, the transformation series of the penultimate segment is difficult to establish. Hence, it is difficult to say how many times the male A1 apophysis have appeared and disappeared within the Parastenocaridinae and if they evolved from absent to incipient towards a strong sickle-shape apophysis or if any other kind of transformation is involved. To be sure, it is necessary to recollect and/or restudy the type species of *Michelicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris, Nanacaris*, *Clujensicaris*, *Minutacaris* and *Lacustricaris*, as well as closely related species and other Parastenocaridinae species not included in this study, since they do not belong and cannot be clearly included within any of the genera currently available taxonomically.

Armature of the apophysis of male P3 (Character 33). The apophysis is generally long and with a distal spine in Fontinalicaridinae, and the spine is usually missing in the Parastenocaridinae (see Schminke 2010). Some exceptions are known. Among the Fontinalicaridinae from the Neotropical region, some species of *Siolicaris* exhibit a short apophysis, and the distal spine of the apophysis is fused or lost in all species of the genus, except for *S. sandhya* (Ranga Reddy 2011). A long apophysis can be observed in *Iticocaris* and in *Brasilibathynellocaris* (Corgosinho et al. 2010a, 2012a), but no trace of a distal spine can be observed in the adult, with the exception of a heteromorphic male of *B. salvadorensis* (Noodt, 1962) and the copepodid V of the same species (Corgosinho et al. 2010a), with a 2-segmented P3 exp with a distal spine not fused to exp-2. *Dussartstenocaris idioxenos* Karanovic & Cooper, 2011, from Australia and *D. bisetosa* Ranga Reddy, Totakura & Shaik, 2016, are two examples of fontinalicaridins without the distal spine in the apophysis of the male P3 exp. Within the Parastenocaridinae, only *Himalayacaris alaknanda* has a distal hyaline spine in the short apophysis. A rounded hyaline cushion can be observed in some species closely related to *Parastenocaris brevipes* (see Reid 1995, Karanovic and Lee 2012a). We have no doubt that the armed apophysis of the male P3 exp is a plesiomorphic character, and the loss of this structure occurred several times within the Fontinalicaridinae This is considered here as a synapomorphy for the Parastenocaridinae, reverting to the primitive condition only in *H. alaknanda*.

The following two characters are considered symplesiomorphies for the Parastenocaridinae.

Inner seta on the basis of P1 (Character 26) The presence/absence of an inner seta on the basis of the P1 has been exhaustively discussed by Galassi and De Laurentiis (2004) and Schminke (2010). This character is considered here as a plesiomorphy for the whole family, disappearing and reappearing only within the Parastenocaridinae. The presence of a very long inner seta on the basis of P1 is an autapomorphy for *Eirinicaris* gen. n.

Shape of the genital operculum (Character 28). A genital operculum which is broader than the height, appears consistently in the females of all the species of Parastenocaridinae studied so far. Interestingly, at least two types of genital operculum are evident within the Parastenocaridinae. In *Eirinicaris*, *Simplicaris* and *Kinnecaris* (see Karanovic and Cooper 2011) the copulatory pore is covered by what Galassi and De Laurentiis (2004) described as “strongly sclerotized operculum represented by a single laminar plate running transversally across the genital double-somite”. The copulatory pore is not covered completely by such plate in *Parastenocaris*. Instead, two lateral discrete plates representing the vestigial P6, form a sclerotized plate, partially covering the genital aperture and the median copulatory pores in *Parastenocaris* (see Karanovic and Lee 2012a).

Ranga Reddy et al. (2014) proposed a division of the Parastenocaridinae into two basic monophyletic groups: one composed by *Himalayacaris*, *Remaneicaris* and the *Parastenocaris tirupatiensis*-group (*Indocaris*), and a group composed of the remaining Parastenocaridinae, called here the crown-group. Our phylogenetic study confirms that Ranga Reddy’s et al. (2014: 813) characters 34 (position of outer setae on third exopodal segment of leg 4) and 35 (spinules near the insertion of the endopod of male leg 4) support the clade formed by *Himalayacaris*, *Remaneicaris* and *Indocaris* as proposed by Ranga Reddy et al. (2014). Characters 38 to 41 appear convergently in two monophyletic groups (*Remaneicaris-Indocaris* and *Kinnecaris-Monodicaris*). Character 37 is an autapomorphy for *Himalayacaris*. Character 50 is autapomorphic for *Remaneicaris*. Character 62 is autapomorphic for *Kinnecaris*. For a discussion on the relationships within this group see Ranga Reddy et al. (2014).

The crown-group is supported in the present study by character 44 (ornamentation of the basis of the male P4) and character 45 (length of the apophysis of the male P3). These are discussed below.

Ornamentation of the basis of the male P4 (Character 44). A row of spinules on the basis of the male P4 close to the insertion site of the enp appears in derived groups within *Remaneicaris* (Corgosinho et al. 2010b; group D). It is absent in *R. ignotus* (Dussart, 1983), *R. meyerabichi* (Noodt, 1962), in the *R. argentina*-group (Corgosinho et al. 2010b; group A), and in the *R. analuizae*-group (Corgosinho et al. 2010b; group C). This character appears as a row of slender spinules inserted in a weakly chitinized zone in derived *Remaneicaris* groups; however these spinules are often omitted in original descriptions (Corgosinho et al. 2007). This ornamentation consists of strong petaloid elements in *Indocaris*, and increase in size from the inner to the outer margin, and is not as complex as in *Parastenocaris*. This ornamentation is not present in the ground pattern of *Remaneicaris*, and our phylogenetic hypothesis does not support the presence of such ornamentation in the groundpattern of the clade (*Himalayacaris* (*Remaneicaris*, *Indocaris*)). Therefore, the strong ornamentation on the basis of the enp is considered here a synapomorphy for the crown-group, occurring convergently in *Indocaris*.

Within the crown-group, this character evolves into a strong row of unequal spinules in *Stammericaris*, *Cottarellicaris* and *Monodicaris*. These spinules are strongly sclerotized and unequal in *Parastenocaris*, slender in *Kinnecaris* and are missing in *Eirinicaris*. Strong unequal spinules are present in *Kinnecaris giselae* Schminke, 2008. The condition observed in species of *Cottarellicaris*, *Stammericaris*, and in other species such as *P. palmerae* Reid, 1992, is not homologous to the condition observed for *Parastenocaris brevipes* and closely related species. In *Parastenocaris*, the spinular complex involves sclerotization, heteromorphy of the spinules, and the presence of anterior and posterior spinules on the basis. With exception of the enlargement and sclerotization of some spinules, nothing similar has been observed for *Cottarellicaris*, *Stammericaris*, and *P. palmerae*.

Length of the apophysis of the male P3 (Character 45). *Remaneicaris*, *Indocaris* and *Himalayacaris* have short apophyses which are, in general, as long as wide. Exceptions for this can be observed in *Indocaris inopinata* Ranga Reddy, Totakura & Shaik, 2016, and in *Indocaris tirupatiensis* (Ranga Reddy 2011). The shortest apophyses are found in *Indocaris imbricata* Ranga Reddy, Totakura & Shaik, 2016, and in *Himalayacaris alaknanda* Ranga Reddy, Totakura & Corgosinho, 2014, and in basal members of *Remaneicaris,* with some exceptions occurring in species belonging to more derived groups within *Remaneicaris* such as *R. membranaceae* (Noodt, 1965) and *R. oncophora* (Noodt, 1965) (Noodt 1965, Corgosinho 2007). The elongated apophysis seems to be also a derived character in *Indocaris*. Interestingly, *I. inopinata* displays an intermediate condition between *I. imbricata* and *I. tirupatiensis.* Hence, it seems more parsimonious to assume a shorter apophysis for the ground pattern of the Parastenocaridinae. A longer apophysis is a synapomorphy for the crown-group, and a convergent short apophysis appears both within the basal Parastenocaridinae as well as within the crown-group (viz. *Cottarellicaris*).

Following the above reasoning, the crown-group as defined here, can be divided into *Michelicaris* and two large monophyletic groups composed by the following genera:

a) Group-1: *Stammericaris*, *Cottarellicaris*, *Italicocaris*, *Entzicaris*, *Horstkurtcaris*, *Macacocaris, Nanacaris*, *Asiacaris*, *Clujensicaris, Simplicaris*, *Lacustricaris,* and *Minutacaris*;
b) Group-2: *Parastenocaris*, *Kinnecaris*, *Monodicaris,* and *Eirinicaris*.

Group-1. The monophyly of group-1 is supported on the ground of a complex series of transformations of the male P4 enp (Character 67).

Four main monophyletic subgroups were identified within group-1: (*Stammericaris*, *Cottarellicaris*); (*Italicocaris,* (*Entzicaris, Horstkurtcaris*)); *Macacocaris;* and ((*Clujensicaris,* (*Asiacaris, Nanacaris*)), (*Minutacaris,* (*Simplicaris, Lacustricaris*))).

Schminke (2013) redefined the genus *Stammericaris* and proposed *Cottarellicaris* to encompass similar species belonging to obviously distinct subgroups. Although Schminke correctly described and discussed in detail the diagnostic characters he proposed to each genus, he was reluctant to explicitly discuss the synapomorphies for both genera. However, he clearly defined the complex P4 enp as a character common to *Stammericaris* and *Cottarellicaris*. The presence of a seta or lamella inserted distally on the male P4 enp with a proximal bifurcation (what we call here "Y"-shaped enp) (Character 64) and the presence of at most two spinules on the proximal outer margin of the male P3 (Character 78) are considered here as synapomorphies for *Stammecaris* and *Cottarellicaris*. The "Y"-shaped enp is not exclusive for *Cottarellicaris* and *Stammericaris*, but can be also found in *Parastenocaris palmerae*. However, Karanovic and Lee (2012) attributed this species to *Parastenocaris* on the basis of the presence of hyaline processes on the inner margin of the basis of the male P4. We have discussed above the condition of this ornamentation within this group and we agree with Schminke (2012), not supporting the inclusion of *P. palmerae* in the genus *Parastenocaris*. Some of the characters proposed by Karanovic and Lee (2012a) are symplesiomorphies, allowing the inclusion of unrelated species within the genus *Parastenocaris.* As correctly mentioned by Schminke (2013), Reid (1995) conceded that the structure of the endopod P4 male complex and the long and spinulate endopod P4 female could be taken as an indication that *P. palmerae* is part of the *brevipes*-group, but she argued that the short female genital field, the P3 male and the setation of the caudal rami speak against it. In our view, the length of the female P4 enp and the shape and setation of the furca of *P. palmerae* clearly points against the inclusion of this species in *Par-*

astenocaris. Additionally, *P. palmerae* should be included in a group of species closely related to *Cottarellicaris* and *Stammericaris* as proposed by Schminke (2013), based on similar morphology of the male basal ornamentation shape of the "Y-shape-like" endopod of male P4, and similar morphology of the male P3 of *Stammericaris* and *P. palmerae*, sharing a long apophysis and shorter thumb, convergently appearing as autapomorphy for *Stammericaris* and as synapomorphy for a monophyletic group composed by (*Macacocaris*, ((*Nanacaris*, (*Asiacaris*, *Clujensicaris*)), (*Minutacaris*, (*Simplicaris*, *Lacustricaris*)))) (Character 66). Character 78 is discussed by Schminke (2013), who describes a maximum of one proximal and four distal spinules for *Cottarellicaris*, and two proximal and eight distal spinules for *Stammericaris*.

Italicocaris, *Entzicaris* and *Horstkurtcaris* share a P3 apophysis with a "recorted" outer margin (Character 68, shape of the apophysis on the male P3 exp), proximally dilated, with a median depression and a thinner distal lamella. It is important to stress that Karanovic and Lee's (2012b) diagnosis to the genus *Horstkurtcaris* is not supported by a single synapomorphy. Some characters such as "Male antennula seven-segmented, prehensile, with geniculation between third and fourth and fifth and sixth segments" are the result of inaccurate descriptions, since the male A1 is never seven-segmented in Parastenocarididae (Corgosinho et al. 2007). Additionally, the geniculation always occurs between 4th and 5th segment, and between 6th and 7th segments. Therefore, the use of the generic name *Horstkurtcaris* should be restricted to *H. nolli* (Kiefer, 1930) and *H. nolli alpina* (Kiefer, 1960) only, pending a revision and phylogenetic study of the Parastenocaridinae at the species level. The similarities between *Entzicaris* and *Horstkurtcaris* are considerable. Both *H. nolli* and *Entzicaris entzii* (Toeroek, 1935) share the morphology of the male P3, with an enpsigmoid in shape, curved to the inner margin (Character 70 in this study); the male P4 of *E. entzi* is different to that of *H. nolli* in the presence of a single spinule on the basis close to the insertion of the endopod. The female limbs are slightly different in ornamentation and length of the endopod, and both species possess a long furca with all the elements inserted distally. A remarkable difference can be observed in the male P5, being shorter, with the setae inserted distally, and with a feeble inner spiniform process in *H. nolli*. Chappuis (1940) showed a larger P5 of *H. nolli* with a conspicuous inner spiniform process, similar to what was described for *E. entzii*. These astounding similarities suggest that *H. nolli* and *E. entzii* are geographical variants of the same widely distributed species.

The third is composed solely by the genera *Macacocaris*; the fourth subgroup is composed by *Clujensicaris, Asiacaris*, *Nanacaris, Simplicaris*, *Minutacaris*; and *Lacustricaris*. In most of these species the male P3 exp is slender, slightly curved towards the inner margin, the apophysis is elongate, blade-shaped, with a rounded tip, without distal seta; the thumb ranges from smaller than the apophysis (Character 66; 0→1) as in *Simplicaris*, *Minutacaris*, *Nanacaris*, and *Clujensicaris*), to larger than the apophysis (Character 66; 1→0) as in *Asiacaris*. The monophyly of the group composed of *Nanacaris*, *Asiacaris*, *Clujensicaris*, *Minutacaris*, *Simplicaris* and *Lacustricaris* is supported by the presence of a short spiniform enp of the male P4 (Character 67), which is lost in *Nannacaris*, *Asiacaris* and *Clujensicaris*. This group also diplays a trend towards the reduction or loss of the armature of the basis of the male P4 as in *Asiacaris* and *Clujensicaris* (Character 44). This character appears convergently in *Himalayacaris alaknanda*. However, the male P4 enp is not completely lost in *H. alaknanda*, appearing as an inner uncinate bud on the basis.

The phylogenetic position of *Macacocaris* is difficult to decipher. *Macacocaris* shares many characters with other genera, such as the short enp of the male P4 (Character 63) as in *Monodicaris,* the pitted cuticle (Character 61) as in *Kinnecaris* and *Monodicaris*, strong and unequal ornamentation of the inner basis of the male P4 as in *Monodicaris*, *Parastenocaris*, *Stammericaris* and *Cottarellicaris*, and the dimorphic P5 (shorter in the male, with the elements arranged distally as in *Parastenocaris*). Additionally, the males of the genus *Macacocaris* males possess a strongly transformed A1, which Chappuis (1952) describes as "fortement préhensiles", probably similar to what can be observed for *Kinnecaris* and *Monodicaris.* Pending a full morphological and molecular study of this genus, and the redescription of *Macacocaris macaco* (Chappuis, 1952), its phylogenetic position is as inferred in the cladogram (Fig. 9).

Group-2. This group is composed of the genera *Parastenocaris*, *Kinnecaris, Monodicaris,* and *Eirinicaris.*

Schminke (2009) recognized the similarities and close relationship of *Kinnecaris* with *Monodicaris.* The recognition of the closer relationship between *Kinnecaris* and *Parastenocaris* can be traced back to Lang (1948), who pointed to the closer relationship between the *P. brevipes*-group and the *P. muscicola*-group, the latter composed at that time of *Kinnecaris caffer* (Chappuis, 1936) and *K. muscicola* (Chappuis, 1936).

> "The *Brevipes*-group must be closely related to the *Muscicola*-group. The enp of P4 is built in the same way in both groups, however, the *Brevipes*-group, which is the most derived group of both, have kept the basal tooth or finger-like processes." (free translation from Lang 1948, p. 1219).

Parastenocaris, *Kinnecaris* and *Monodicaris* share the tapering furca in the male and female in which the lateral setae I, II and III, and the dorsal seta VII are situated in the middle of the rami, setae I, II and III opposite to seta VII (Characters 46 an 47, for the male and female, respectively). The tapering furca and the position of setae I, II, and III aligned opposite to seta VII is observed in the female of *Eirinicaris* (Character 48), changing position of setae I, II, and III, their relative position to

seta VII (with a large gap between them), the shape and ornamentation of the furca in the male as the result of the extreme dimorphism.

Eirinicaris is closely related to *Kinnecaris* and *Monodicaris*. These three genera share the long spiniform process on the male and female P5, reaching beyond the middle of the second (genital) urosomite (Characters 55 and 56 for the male and female, respectively), and proximal insertion of the lateral setae on the female. An interesting character, which was previously described for *Kinnecaris* by Karanovic and Cooper (2011), is the presence of a pore at the distal rim of the inner acute spiniform process of the P5 (Character 76). This pore is also present in *Eirinicaris*, but was not described for *Monodicaris*. The recent observations of an undescribed species of a new genus from Brazil (Corgosinho and Previattelli, pers. obs.) revealed the presence of this pore on the male P5. This is an indicative that this pore is widely distributed within the family, making possible that it could have been overlooked in *Monodicaris*.

On the morphology of *Eirinicaris* gen. n. *Eirinicaris* gen. n. is an intriguing genus with some unique characters. The basis of the male P1 possesses a very long inner seta, a character never reported for this family before. The telson and furca are very ornate in the males of this species, and the furca exhibits an extreme level of dimorphism with setae I, II and III situated proximally on the ventral side of the furca. Spinular ornamentation on the telson and furca is not uncommon within the family. The presence of spinular ornamentation on the telson is present in species closely related to the parastenocaridin *R. analuizae* Corgosinho & Martínez Arbizu, 2005 and *R. tridactyla* Corgosinho, Martínez Arbizu and Santos-Silva, 2007. Other species within this subfamily such as *P. spinicauda* Wells, 1964, *P. spinosa* Wells, 1964, *P. trisaetosa* Chappuis, 1954, also possess spinular ornamentation on the telson. Within the Fontinalicaridinae, *Parastenocaris nigerianus* Chappuis, 1959 and some species of *Forficatocaris* exhibit spinular ornamentation of the telson. Concerning the furca, normally the modification occurs in females (Schminke 1976). Such high levels of ornamentation on the telson and furca have never been described for the family. Similar levels of ornamentation can be observed only in freshwater Canthocamptidae Brady, 1880.

Equally impressive is the level of modification of the posterior seta of the last segment of the A1, the endopod of the P3 and the furcal setae I, II, and III in the males. The last segment of the male A1 possesses an additional modified aesthetasc-like seta ventrally. Additionally, the enp of the male P3, and the furcal setae II and III are transformed into aesthetasc-like structures. Within the Copepoda the aesthetascs are generally restricted to the A1. Aesthetascs are also present in the mouthparts of some Paranannopidae Por, 1986 (Gee and Huys 1991). To our knowledge, this is the first species of Copepoda with aesthetascs-like setae on the furca and leg 3 of male.

Distribution and ecology. Prior to this study, *Remaneicaris* was the only representative of Parastenocaridinae in the Neotropical zone. The discovery of *Eirinicaris* in Brazil extends the geographical distribution of other monophyletic groups of Parastenocaridinae to South America, hence, indicating that all the main phylogenetic lineages of Parastenocarididae were already present in a vast geographical area, before the split of Pangea.

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